The Hot and the Classic

Plant Thermogenesis and Thermoregulation

One of the drawbacks of our current preoccupation with model organisms and our inveterate focus on crop plants is that our natural curiosities about some of the more bizarre plants in the world go largely unsatisfied. I suspect that many readers of this journal were inspired to become plant physiologists when they first observed time-lapse images of a climbing tendril, or touched a *Mimosa pudica* plant, or, usually with disappointing results, fed their first fly to *Dionaea muscipula*. Plant movements and plant carnivory are two examples of plant functions that, in a grand and anthropocentric view of life, are in themselves not terribly important. Their fascination to us (and to the minds of children) lies in the fact that these seemingly animal-like behaviors challenge our preconceived notions of what plants are capable of doing, and make us appreciate, often for the first time, that the plant and animal kingdoms have more in common than they do differences.

A third plant function that the uninitiated often expect is limited to the animal world is thermogenesis. The most dramatic examples of plant thermogenesis occur in certain types of flowers, particularly, but not exclusively, in the Araceae. Although most studies of plant thermogenesis have examined Araceae, it must be borne in mind that thermogenesis has been measured in the flowers of members of eight other angiosperm families as well as in the cones of various species of cycads (Thien et al., 2000). There is some evidence that thermogenesis, albeit at rates much less than those observed in thermogenic flowers and cones, may be a property of most plants. It should also be noted that some plants, including *Philodendron selloum* (Nagy et al., 1972), eastern skunk cabbage (*Symplocarpus foetidus*) (Knutson, 1974), the sacred lotus (*Nelumbo nucifera*) (Seymour and Schulze-Motel, 1996, and *Rhizanthes lowii*MDNM^{-} (Patino et al., 2000) can thermoregulate: They can alter their thermogenic properties to maintain a surprisingly constant temperature even under fluctuating environmental temperatures.

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The Raison d'Être of Thermogenesis

Many reasons for the occurrence of thermogenesis in flowers have been put forward. Thermogenesis may ensure protection of flowers during periods of cold temperature. For example, the spadices of eastern skunk cabbage are not frost-resistant, even though they can emerge from snow-covered ground (Knutson, 1974). Avoiding frost damage, however, cannot be the primary function of thermogenesis: Most members of the Araceae are tropical species that would have no need to escape frost in nature. Rather, frost-avoidance by thermogenesis may reflect a physiological exaptation of a process that originally evolved in response to selective pressures other than frost. Other researchers have suggested that thermogenesis and thermoregulation may help provide the optimum temperature for floral development or pollen tube growth (Ervik and Barfod, 1999). Seymour and Blaylock (1999) found that warming did advance the development and early flowering of eastern skunk cabbage but pointed out that the adaptive value of this was obscure: Many plants were observed completing their blooming beneath a layer of forest litter and sometimes a layer of snow.

Other hypotheses concerning the raison d'être of thermogenicity in flowers have focused on the effects it may have in attracting pollinators. The heat produced by thermogenic flowers helps to volatilize odorous compounds that attract carrion flies, beetles, and other insects, and there is a strong temporal correspondence between thermogenicity and the release of such odors (Lamprecht et al., 2002). More than 100 compounds from at least nine different chemical classes (monoterpenes, sesquiterpenes, fatty acids, ketones, alcohols, aldehydes, indole, and phenolic and sulfur compounds) are liberated during the thermogenic activity in voodoo lily (*Sauromatum guttatum;* Skubatz et al., 1996) Electron microscopy revealed that the endoplasmic reticulum (ER) interacts with the plasma membrane, creating novel routes of excretion of the volatiles to the exterior of the cell. The foul odor produced by the appendix attracts at least 30 species of insects. In the case of temperate-zone, early flowering skunk cabbage, however, there is a paucity of good insect pollinators to attract and, in fact, in the case of Symplocarpus renifolius, only 13% of the spadices set seed (Uemura et al., 1993).

In addition to attracting insect pollinators by smell, thermogenic flowers may also attract insects by heat. The floral temperatures of thermogenic plants are in the range required by endothermic insects for purposes of mating and flight (Schneider and Buchanan, 1980; Seymour and Schulze-Motel, 1997).

Mechanism of Plant Thermogenesis

It has long been known that thermogenesis is linked to a burst of cyanide-resistant respiration involving the alternative oxidase pathway (James and Beevers, 1950; Meeuse, 1975). Classical studies revealed that heat production usually begins first in male flowers and then spreads throughout the inflorescence. It was hypothesized that this pattern was a reflection of the movement of a chemical signal "calorigen." Salicylic acid may be "calorigen": it triggers an increase in the alternate oxidase and heat evolution in the voodoo lily (Raskin et al., 1987), but it has it not been demonstrated that it moves in the same manner as "calorigen." In fact, it may be the sensitivity of the tissue to salicylic acid that increases daily with the approach of anthesis (Raskin et al., 1987).

How Widespread is Plant Thermoregulation?

Many but not all plants increase alternate oxidase activity at low temperatures (e.g., Ito et al., 1997; Gonzalez-Meier et al., 1999;). Salicylic acid also increases alternate oxidase, alternative respiration and heat production in tobacco suspension cell cultures (Kapulnik et al., 1992; Rhoads and McIntosh, 1993). It has been postulated that the alternative respiratory pathway may help to maintain mitochondrial electron transport at low temperatures that would otherwise inhibit the main phosphorylating pathway and lead to the formation of toxic reactive oxygen species. This role is supported by the observation that alternative oxidase protein levels and alternate oxidase activity often increase when plants are subjected to growth at low temperatures (e.g., Nevo et al., 1992; Moynihan et al., 1995; Vanderstraeten et al., 1995). Nevo et al. (1992) proposed that thermogenesis resulting from increased engagement of the alternative oxidase pathway may be a genetic adaptation to avoid cold temperatures. When leaf tissues from *Triticum dicoccoides* and *Hordeum spontaneum* were exposed to low temperature, metabolic heat rates measured at 20°C increased markedly as a result of cold treatment. This response was cultivar specific, the response being greater in accessions from colder regions. Besides preventing free radical damage, another way that thermogenicity might help plants exposed to cold temperatures to survive is by heat itself: Sometimes a fraction of 1°C is all that is necessary to protect a plant from cold damage. Nevertheless, Breidenbach et al. (1997), while not contesting the increase is heat given off by some chilled plant species, criticized the idea that the alternative pathway is thermoregulatory and serves to protect plants from exposure to cold. They argued that the different oxidative pathways in the mitochondria do not have large differences in enthalpy, and that the observed heat rate increases are insufficient to cause significant temperature increases of physiological importance in non-thermogenic plants.

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